

Microarmature and Barriers in the Aperture of Land Snails

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(5 Plates)

DEVELOPMENT OF VARIOUS FOLDS, ridges, calluses, tubercles, constrictions or lamellar plates that effectively narrow the shell aperture is a common phenomenon in non-operculated land snails. With the obvious exception of slugs or taxa with partly (Succineidae, Vitrinidae) to drastically (some Helicarionidae, Testacellidae) reduced shells and visceral humps, most families show at least a few species with apertural narrowing caused by such constrictions. There is no agreed nomenclature for these structures, which have most frequently been cited as "teeth". Since this has obvious gustatory connotations, a better term for general usage would be to refer to these as "barriers". This generic term can be modified to indicate the form of the structure by use of the more traditional terms as modifiers.

The general assumption has been that these barriers are effective in reducing predation by arthropods (see COOKE, 1895: 63). Along with the production of distasteful mucus by slugs, an offensive odor (as in *Oxychilus*, see LLOYD, 1970), issuing an irritating froth or liquid (as in *Liguus*, see EISNER & WILSON, 1970), and self amputation of the posterior tail (as in *Prophysaon*, see PILSBRY, 1948: 680), such barriers are a basic defense mechanism of pulmonate snails. They are partial substitutes for the operculum of prosobranchs, which forms a nearly impregnable defense against small predators.

The number, position, shape and size of these barriers frequently has been used as identification or diagnostic features for both genera and species, particularly in such groups as the Clausiliidae, Tornatellinidae, Urocoptidae, Endodontidae (*s.l.*) and Pupillidae (*s.l.*) where the shell is rather uniform in appearance. Virtually no attention has been paid to their structure and formation. The development of "prickly nodes" on apertural lamellae in *Strobilops* (PILSBRY, 1948: 862, fig. 466), calcareous hooks that point towards the outside of the aperture on the lamellae

in *Thaumatodon multilamellata* (Garrett, 1872) (see PILSBRY, 1893-1895: plt. 4, fig. 38), plus numerous observations on the internal ridges in various Urocoptidae are among the few exceptions.

Scanning Electron Microscope (hereafter SEM) examination of barriers and apertural surfaces in several land snail families has shown that a high percentage of species have microarmature, not just on the barrier edges, but over much of the lip surface, particularly the columellar and parietal regions of the aperture. This report is concerned with the basic pattern of such microarmature, its probable function, and how more sophisticated microarmature could have evolved from the generalized condition. As necessary background information, a brief survey of barrier types is presented. A second report (SOLEM, in press) will discuss structural differences in the armature found on the barriers in species of Charopidae and Endodontidae.

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Patterns of Apertural Narrowing

There is no single strategy for barrier formation, but rather a great variety of experiments. Most involve deposition of calcareous ridges, inward lip edge growth, or a combination of both. Large and complex barriers can be present in early and mid-juvenile stages, then become greatly reduced to absent in the adults. The Tornatellinidae (see COOKE & KONDO, 1960: 113, figs. 50, a, d, e), Cerionidae (see PILSBRY, 1946: 161, fig. 76), and zonitoid taxa such as *Ventridens* (see PILSBRY, 1946: 438, fig. 235) exemplify this approach. These barriers are formed early, added to anteriorly and resorbed posteriorly during juvenile growth, and then mostly resorbed before or when the animal reaches terminal size. In other groups, such as the Urocoptidae, Strobilopsidae, Charopidae and Endodontidae, the barriers may be formed early, growth follows the same pattern as in the first type, but then the barriers are retained at essentially full size during the adult stage.

Perhaps most common is for the juvenile shell to totally lack any barriers or constrictions of the aperture, with the adult animal secreting complex barriers upon reaching maximum size. Such families as the Pupillidae (*s.l.*), Strep-taxidae, Odontostominae and Polygyridae (especially *Polygyra*, *Stenotrema* and *Triodopsis*) have a majority of species with well developed barriers. Frequently only a few genera in a family will show this development. Bulimulid genera such as *Auris*, *Eudolichotus* and *Otostomus*, camaenid genera such as *Labyrinthus*, *Traumatophora*, *Moellendorffia* and most of the West Indian derivatives from *Pleurodonte*, bradybaenid taxa such as *Metodontia*, *Semibuliminus*, *Pseudaspasita* and *Odontotrema*, and various European helioid taxa have greatly developed apertural barriers although most taxa in these families have not or only slightly constricted apertures. Even in the helicarionid taxa, genera such as *Brazieria* and *Sesara* depart from the normal open aperture by developing high, transverse lamellae. Occasionally as in some pupillids,

juveniles will have one form of barriers and adults a totally different set.

A few taxa build barriers at regular intervals. In *Helicodiscus* (see PILSBRY, 1948: 626, fig. 339, b) there are tubercles at about quarter-whorl intervals. Apparently these are not resorbed, or only resorbed after several new barriers have been erected. Members of the Corillidae have carried this approach to its logical conclusion. Highly complex barriers are "... formed on the completion of each half of a whorl, after which the previous set is absorbed by the animal. I have observed several specimens which contained two sets of barriers at a distance of half a whorl; in some cases the older set had almost vanished ..." (GUDE, 1914: 55).

Finally, the clausilium and barriers found in members of Clausiliidae and the most unusual apertural closing attributed to *Thyrophorella* from Sao Thomé, a hinged flap (see GIRARD, 1896), are additional strategies for apertural narrowing.

All of these barriers should be viewed as representing structures partly compensatory for the absence of the prosobranch operculum. That is, they hinder possible predators from reaching the animal after it retreats behind the barriers. This was perhaps suggested first by GUILDING (1829: 168) in an oft quoted sentence—"I know not whether the use of the teeth and laminae of the *Pupadae* (=Pupillidae, *s.l.*) has been explained; they may answer the purpose of an operculum to keep out enemies, while they afford no obstacle to the motions of the soft and yielding body of the animal." Subsequently GODWIN-AUSTEN (1874: 611) reported finding small insects stuck between the barriers in two specimens of the corillid genus *Plectopylis*. While not frequently observed, anybody who has sorted field collections of small land snails that have large and complex apertural barriers can attest to the reality of this phenomenon.

At times the barriers come so close to filling the aperture of the shell that it is difficult to conceive how the buccal

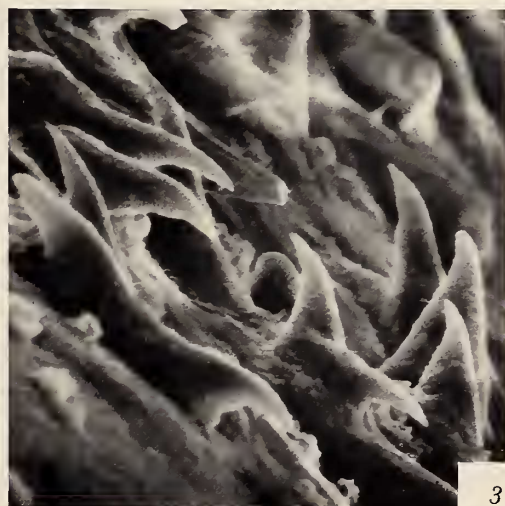
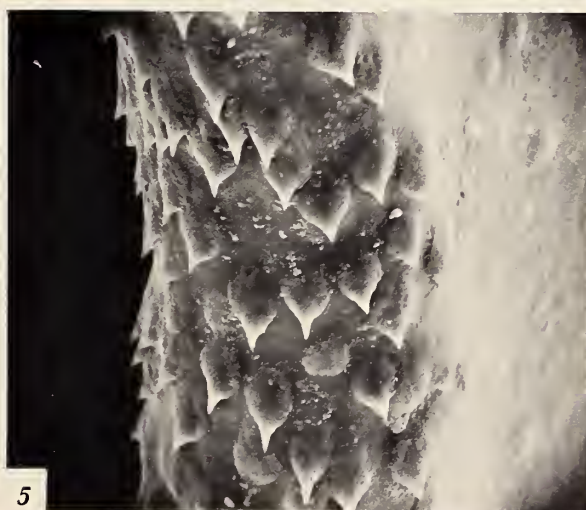
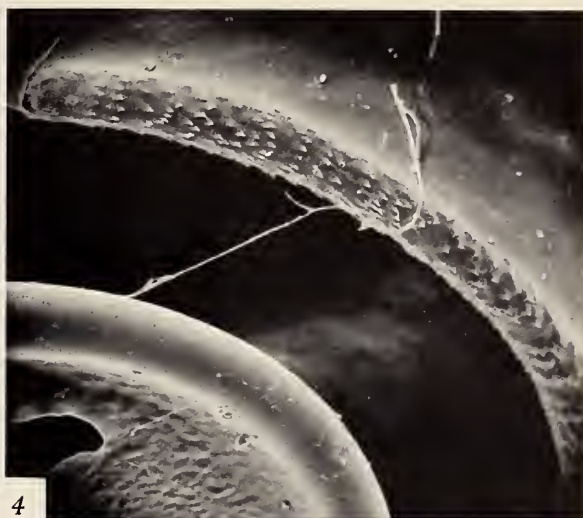
Explanation of Figures 1 to 6

Tornatellina plicosa Odhner, 1922

Figures 1 to 3: Southwest slope at 500 - 530m elevation, Portazuelo, Masatierra, Juan Fernandez Islands. Field Museum of Natural History number 167976. Figure 1: partial view of shell aperture at 76 \times showing columellar (upper center), parietal (lower right center), and lower palatal (bottom center) lamellae. Figure 2: lower side of outer edge of columellar lamella at 880 \times showing concentration of microdenticles on sides of lamellae. Figure 3: part of a cluster of denticles from same area at 4230 \times .

Tekoulina pricei Solem, 1972

Figures 4 to 6: Station R-11, summit of Mt. Te Kou, Takuvaine Valley, 1930 feet elevation, Rarotonga, Cook Islands. Field Museum of Natural History number 153414. Figure 4: Palatal (upper with serrations) and columellar (lower and smooth) lamellae near posterior end of palatal (upper left) at 139 \times . Figure 5: Surface of palatal lamella at 826 \times showing positioning of denticles on upper surface. Figure 6: Details of denticle shape and relation to surface of lamella at 4646 \times .



mass and muscular foot can be successfully withdrawn and protruded. In the polygyrid genus *Stenotrema* (Figure 23), for example, the aperture is effectively narrowed to a thin slit by lip extensions and a parietal lamella. In such Florida species as *Polygyra uvulifera* (Shuttleworth, 1852) and *P. auriculata* Say, 1818 (see PILSBRY, 1940: 595, fig. 384) the degree and complexity of constriction is even greater. In many of the minute Tornatellinidae (for example, COOKE & KONDO, 1960: 107, fig. 47, a-c), Pupillidae (for example, see PILSBRY, 1948: 897), and endodontoid taxa (SOLEM, in press, figs. 1-6) high lamellar barriers come close to overlapping in the middle of the aperture. Such structures are not limited to minute or medium sized land snails. *Labyrinthus otis* (Lightfoot, 1786) is a South American camaenid ranging from 39-54 mm in diameter. A combination of a raised parietal lamella and a huge palatal tubercle that shows on the outside of the shell as a deep indentation combine to grossly restrict the shell opening (see SOLEM, 1966: 110, fig. 30, b). The internal barriers of the 10-25 mm *Plectophyllis* are equally effective (see GUDE, 1914: 87, fig. 35).

There is no simple relationship between relative size of the barriers and the size of the organism. In the Polygyridae, small sized genera such as *Polygyra* and *Stenotrema* (see ARCHER, 1948) do have large barriers, while the larger *Triodopsis* and *Mesodon* have reduced or vestigial denticles. However, the small *Praticolella* whose distribution overlaps that of *Polygyra* and *Stenotrema*, totally lacks such barriers. In the Pupillidae (*s. l.*) the minute *Vertigo* and relatively large *Pupilla* lack barriers or have very small ones, while the extremely complex barriers occur in the medium sized *Gastrocopta*. In contrast, the larger species of *Labyrinthus* have proportionately larger barriers than do the small species (SOLEM, unpublished data). What is needed before relative barrier size can be interpreted functionally is hard data on the predators of particular species. Unfortunately, this is mostly unavailable.

Arthropod Predators and Barrier Effectiveness

While it is a text book statement that snails are preyed upon by carabid beetles, larval fire flies, silphid beetles, and various sciomyzid flies, we know nothing concerning the identity of predators on micro-species. Essentially all published records are about larger insects feeding on European or North American helicoid and zonitoid taxa. Predaceous mites, the smaller staphylinid beetles, plus a huge variety of less familiar groups belonging to the litter fauna are potential suspects. Until these receive more study,

analogies will have to be drawn from data on the larger snail-eating insects.

Carabid beetles, both adult and larval stages, are active predators on medium to large sized land snails. Indeed, one tribe, the Cychrini, is almost exclusively malacophagous. Data concerning both adult and larval feeding patterns in *Carabus* have been given in a recent review (STURANI, 1960). The larva or adult enters the snail's aperture (STURANI, 1960: 94, fig. 6), gradually consuming the occupant. In some cases, pieces of the shell are broken off to facilitate feeding (STURANI, 1960: 123, fig. 14; p. 136; p. 140, fig. 23). Similar patterns are shown by the snail-eating Silphidae. Both narrowing and elongation of the head and thoracic region are associated with this habit. In an elegant paper, BOETTGER (1921) demonstrated coevolution between predator and prey, with increasing size of palatal aperture barriers in the North African helicid snail *Otala (Deserticola) tigris* (Gervais, 1857) countered by decreased width of head and thorax in the carabid beetle *Carabus morbillosus* Fabricius, 1792.

Considerable information about larval feeding on snails in the lampyrid beetles *Lampyris* and *Phausis* is given by SCHWALB (1961: 456-470), including experimental tests concerning prey location and method of attack.

The significant feature in both the carabid and lampyrid method of feeding is that efficient utilization of the food source requires the predator entering or breaking the shell at some point. If a crawling snail is caught and the head and extended foot bitten or pulled off, considerable volume of the snail still remains inside the shell. For a small predator that cannot crush the shell, only entry into the aperture permits utilizing this part of the prey. If the snail is retracted into the shell, then it is available to the predator only by entering the aperture. Hence the evolution of barriers behind which the snail can retreat would be an effective means of defense. Even if the snail lost a tentacle to an initial grab by a predator, a quick retreat behind the barriers would be effective, if the opening that remained was too small for the predator to gain entry and the predator could not crack the shell.

The utility of such barriers to a particular land snail would depend upon the local predators. Most predators have a size range of objects that are recognized as possible "prey", while things that are smaller or larger than this size are "non-prey". It is also well established that for many predators, the food sources will differ according to the season of the year. Hence the patterns of apertural barriers in land snails that vary from present in adult but absent in juveniles to the exact opposite situation would reflect selective pressure under particular circumstances.

Ornamentation on Apertural Surfaces

With the above background information on the occurrence, age correlation, and function of barriers in larger species of land snails, it becomes possible to discuss the ornamentation found on the surface of these barriers in smaller species. While in some taxa the barriers have shown an absolutely smooth surface even at 2000 \times magnification, in most of the small species there have been marked protuberances. These are particularly well developed in the Endodontidae and Charopidae (Solem, in press). The data reported on here represent only a tiny sampling of the world fauna. It is too early to say that this is an almost universal phenomenon, but the discovery of these structures in more than 85% of the species examined to date suggests that it is very widespread.

Tornatellina plicosa Odhner, 1921 (Figures 1-3) is a very small species, found on ferns or under leaves, from Masatierra, Juan Fernandez Islands. The maximum recorded adult size is 5.1 mm in height. The photographed individual is a 2.47 mm high subadult. Optical measurement of the distance from the outer edge of the basal lip to the upper margin of the parietal lamella (left part of Figure 1) is 0.69 mm. When the surfaces of the major barriers, both top and sides, are examined at 880 \times (Figure 2) and 4230 \times (Figure 3), they are seen to be covered with scattered to densely clustered calcareous hooks and tu-

bercles. The hooks do not form a clear pattern, but lie at a variety of angles from the vertical and point in almost any direction. *Tekoulina pricei* Solem, 1972 (Figures 4-6) from Rarotonga, Cook Islands also is a tornatellinid. It reaches 9.1 mm in height and is a much more elongated species than the *Tornatellina*. Apertural armature is much less complex, with only single parietal, columellar and palatal apertural barriers. The columella (Figure 4, lower left) is smooth, but the palatal lamella (Figure 4, upper right) and parietal (not shown) have the top and upper side covered with raised denticles that point towards the outside of the aperture. Inspection at higher magnifications shows that these denticles have their anterior fifth free of the surface (Figure 6 at 4646 \times) and their outer margin slopes back to the surface at about a 30° angle (left side of Figure 5 at 826 \times). From a broad base, each denticle narrows to an elongated, spear-like tip. Please also note that the surface of the columellar wall (Figure 4, extreme lower left) has vague irregularities.

Barriers in the Tornatellinidae are present when the young hatch, grow anteriorly as the shell grows, and are absorbed posteriorly. The resorption margin on the palatal lamella in *Tekoulina* can be seen at the upper left of Figure 4. Both in structure, orientation and distribution, there are major differences between these two tornatellinids, indicating that variation within family units can be extensive.

Explanation of Figures 7 to 12

Vertigo milium (Gould, 1840)

Figures 7 to 10: Menard County, Illinois. Field Museum of Natural History number 18776: Figure 7: Aperture and body whorl at 74 \times . Figure 8: Lateral view of parietal lamella edge at 2450 \times . Figure 9: View from lower side of parietal lamella at 1879 \times . Figure 10: Vertical view of denticles on parietal lamella at 5980 \times .

Virpazaria adrianae Gittenberger, 1969

Figures 11, 12: "Velika jama," near Soko Mt., near Dupilo, west of Virpazar, Montenegro, Yugoslavia. Rijksmuseum van Natuurlijke Historie, Leiden. Figure 11: Aperture of shell at 79 \times . Figure 12: Edge of palatal barrier at 935 \times .

Explanation of Figures 13 to 18

Strobilops labyrinthica (Say, 1817)

Figures 13 to 15: Below Esterville, West Fork, Des Moines River, Emmet County, Iowa. Field Museum of Natural History number 154121. Figure 13: Parietal lamellae at 195 \times . Figure 14: Lateral view of small denticles at 2090 \times . Figure 15: Detail of a single denticle at 6250 \times showing relationship of denticle and parietal lamellar surface.

Phrixgnathus erigone (Gray, 1850)

Figure 16: Waitakere Range, north of Auckland, North Island, New Zealand. Field Museum of Natural History number 135477. Denticles on columellar wall at 2485 \times .

Dentherona bairnsdalensis (Gabriel, 1930)

Figures 17, 18: Jemmy's Point, Lakes Entrance, Victoria, Australia. National Museum of Victoria, Melbourne. Figure 17: Aperture

of shell with outer lip partly broken off at 73 \times . Figure 18: Low angle view towards posterior of parietal lamellar surface at 2435 \times .

